FLORA AND CHOROLOGY OF THE PINUS ALBICAULIS—VACCINIUM SCOPARIUM ASSOCIATION

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Floristic variation within a plant association may indicate that the habitat of the association is not uniform throughout, and that two or more plant associations are being considered as one, the extreme case being that each community is an individual, an association unto itself. Other interpretations exist; summaries can be found in several texts dealing with vegetation. In this report I shall describe the compositional variation of the *Pinus albicaulis–Vaccinium scoparium* association, and relate some of the variation to one factor of vegetation formation (Major, 1951), i.e., the flora from which the vegetation may have originated.

The suggestion that a single plant association varies according to the flora available to it suggests that this association may exist in more than one floristic region. If regional climate and events during evolutionary time determine floristic regions, one might conclude that these factors could act differentially within the association and thereby affect its variation. Alternatively, if one assumes that a recurring mixture of plant species indicates a particular set of environmental conditions, and that the probability of two or more of these species concurrently evolving the same degree of ecotypic variation is low (at least lower than with a single taxon), then it follows that the habitat within which this association of plant species exists is more or less equivalent throughout (if it is integrated over ecologic time). Thus, if this be the case, floristic differences of communities with "identical" habitats must be a result of either the availability of their flora at the time of their establishment (Egler. 1953) and/or through the remainder of their existence. Major and Pyott (1965) give an interesting review and discussion of this topic. More recently, Westhoff and van der Maarel (1973) and Mueller-Dombois and Ellenberg (1974) have included this aspect of vegetation in their writings.

Methods

Stands in Wyoming, Idaho and Montana with overstories dominated by *Pinus albicaulis*, understories dominated by *Vaccinium scoparium*, and lacking conspicuous populations of *Abies lasiocarpa* seedlings and/or layered shoots (i.e., *Abies* reproduction less than that of *P. albicaulis*), and soils not stony or rocky (Soil Survey Staff, 1976) enough to obviously affect the growth and distribution of plants, were sampled. Within a 600 m² area the coverage of each vascular plant taxon was estimated. Foliose aboreal lichens were also collected, but not systematically. Nomenclature follows that of Hitchcock and Cronquist (1973) for the Pacific Northwest vascular plants, Munz and Keck (1968) for other vascular plants, and Hale (1969) for lichens. Taxonomic authorities not in the text are listed in Table 1.

Results

Four species other than *Pinus albicaulis* and *Vaccinium scoparium* were nearly ubiquitous in the sampled stands: the widespread *Carex rossii*, *Abies lasiocarpa* and *Poa nervosa* with constancies of 80, 90 and 70% respectively, and *Arnica latifolia* (80% constancy, though absent from most Wyoming stands). The presence of these taxa lends some support (or degrees of freedom in a statistical sense) to the initial assumption of the improbability of two or more species concurrently evolving associated ecotypes.

In Table 1, the flora and some other stand characteristics are provided in relevé form. This table lists the stands in a latitudinal sequence, with adjustments to accommodate latitudinally-similar stands with widely separated longitudinal ordinates (cf. Fig. 1). Stands have not been sorted according to their floristic similarities as is usually done in relevé analyses (Mueller-Dombois and Ellenberg, 1974). However, taxa have been arranged to give the maximum impression of latitudinal change to demonstrate that the flora of the association changes clinally with latitude, and that the flora of any stand is at least a *partial* consequence of the floristic region in with the stand exists (certainly other factors are also involved).

Table 1*a* consists of those taxa with constancies > 15%, and whose presence appears to be nonrandomly distributed within the association. When the within-association distributions of these taxa are compared to their general distributions listed in standard Floras for the Pacific Northwest (Hitchcock and Cronquist, 1973; Davis, 1952; Booth and Wright, 1966; Shaw, 1976; Despain, 1975), approximately 15% are found to be distributionally restricted from attaining 100% constancy in the *P. albicaulis–V. scoparium* association. Similarly, of those taxa with between 5 and 15% constancies, and those with < 5% constancy (Tables 1*b* and 1*c*), about $\frac{1}{2}$ of the former and $\frac{1}{3}$ of the latter are distributionally restricted from ubiquity in the association. Taxa which exhibit no latitudinal affinities (Table 1*c*) are characteristically widespread in their general distributions. In total, about 25% of the association flora shows limited general distributions within the area encompassed by the association.

A few taxa in Table 1 deserve special mention. The low glandular shrub, *Leptodactylon pungens*, and the similar but more cushion-like *Arenaria aculeata* both have stiff spinulose leaves often found in desert-region plants, as indeed both are. In *P. albicaulis* forests these species are found in the southern Bitterroot Mountains and the Salmon River Moun-

association due to their actual 'narrow' regional distributions are denoted by asterisks (*). Simple presence in the 600 m² sampling area is rep-TABLE 10. FLORA OF THE 21NUS ALBICAULIS - VACCINIUN SCOPARIUN ASSOCIATION. Stand age (years), % arboreal canopy coverage and % Y. scoparium coverage are shown along with the taxa of the association with constancies greater than 15% (and which exhibit limited distributions within the association). The stands have arranged in a latitudinal sequence from south to north (cf. Fig 1 and text). Assume varietal status of each taxon to be common Rocky Mt. variety or equivalent to specific epithet unless stated otherwise. Taxa with limited distributions within the range of the resented by a '+', whereas '1-5' represent frequency classes from low to high ('4' is the highest recorded value).

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142

TABLE 1b. FLORA OF THE PINUS ALECAULES - VACCINIUM SCOPARIUM ASSOCIATION; TAXA OF THE ASSOCIATION WITH CONSTANCIES BETWEEN 5 AND 15% (AND WHICH

TABLE 1.2. FLORA OF THE FINUS ALEFCAULIS - VACCIVITY SCOPARIM ASSOCIATION; THE TAXA OF THE ASSOCIATION EXHIBITING NO LATITUDINAL AFFINITIES 1.

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1. Thirty-two taxa have only single occurrences in the stands (constancy 5%). In the latitudinal sequence shown above, the stands with their respecer: 28 Ettpa conidentatis Thurb., "Happlopappus suffructioneue (Nurt.) Gray: 27 Eilene vepens Pers.; 15 Goodyera oblongifolie Raf.; 7 Poa alpina L.; Gray. "Lévarthastrea nutallé (Gray) Ewan., "Penstemon flavescers Pennell. Heenacien alhéflorne Hook., Darthanda intermedia Vasey. Hypericum fortive taxa are: 17 Frigeron pumilue Nutt.: 19 "Mertensia viliata (Tort.) G. Don., Gentiana aravella L.: 20 Arenaria of tusikina (Rydb.) Fern., Seiaghella dena escrulorun (Naxon) Tryon, Sarifraga invukialis L.: 10 Pensterron fruticosue fruticosue (Pursh) Greene; 2 "Trifolium haydenti Portmosium nortoniae (Jones) 'litchc., Agoseris glauca aurantiaca (Nook.) Greene, "Spiraea dersifolia Pall., Anaphalis margaritzeea (L.) B. & H.; 23 5 "Vassinium meminaraseun Dougl.; 3 Valeriana edulis Nut., Lloydia sonotina (L.) Sweet: 30 Myropitys monotropa Crantz; 26 "Aster stenomenes Gray. Promus carbactus H. & A.; 25^{tleptodactylon} purgera (Tort.) Nutt.; 24 Arex paueifolis. Nutt., Salix phylicifolia L., *Veronica cusickii larez paysonis Clokey. Pra samibergii Vasey, Festuca ovina brevifolia (R. Br.) Wats.; 22 Companula parnyi Gray. MADROÑO

tains of east and central Idaho. The dry finger-like intermountain valleys (Lemhi, Pahsimaroi and Lost River Valleys) which extend from the northern edge of the Great Basin and abut these mountain ranges probably supplied the migratory path for these species from the deserts to *P. albicaulis* forests. To find either taxon in a mesic subalpine forest is surprising, but would have been much more so if that forest had been in central Montana, rather than east-central Idaho with its direct connection to the Great Basin.



FIG. 1. Distribution of the *Pinus albicaulis-Vaccinium scoparium* association. The numbers and their associated characters (e.g., n-, -n-) represent stand numbers and the three geographic/floristic regions referred to in the text. The geographic extent of the stands is thought to depict the range of the association. The unhatched area inside the dotted line represents the gap in the distribution of *Pinus ponderosa* (from Little, 1971). (There is no Stand 21).

Three species of the *P. albicaulis–V. scoparium* association are relatively narrow endemics: *Penstemon flavescens* (Idaho Co., Idaho and Ravalli Co., Montana), *Chionophila tweedyi* (central Idaho and adjacent Montana), and *Aster stenomeres* (central Idaho and adjacent Montana to northeastern Washington and southeastern British Columbia). These taxa would not be expected to occur in whitebark pine stands outside their restricted ranges. Similarly, the typically alpine *Trifolium haydenii* extends only as far north as southern Montana. It occurs in a whitebark pine stand immediately adjacent to alpine meadows and scree in the Madison Range (Gallatin Co., Montana) and would not be expected in *P. albicaulis* forests farther north.

Though the general regional occurrences of the above taxa are easily obtained from standard Floras, their equally important intraregional distributions are not so readily available. For example, *Arnica latifolia* and *Carex geyeri*, which are prominent in many Montana whitebark pine stands, are absent from the stands in the Wind River Mts. This mountain range does support both taxa but their populations are not as extensive as elsewhere. In such cases the chance of limited taxa reaching *Pinus albicaulis* forests is low. King (1977) has noted this same phenomenon but on a much smaller scale; the ability of a plant to colonize ant mounds in British pastures is determined by its relative abundance and distance from the mounds.

Lichens. Both Letharia vulpina (L.) Hue and Hypogymnia vittata (Ach.) Gas. were widespread throughout the association, the former being much more prominent. Alectoria oregana Tuck. and A. americana Mot. were confined to the northern-most stands. Both alectorias have limited distributions in the Rocky Mts. which correlate with their presence in the whitebark pine forests.

Ecological Factors. Ecological factors (s. strictu) do, of course, differ somewhat between stands, and plants respond accordingly. For instance, whitebark pine forests in the Wind River Mts. of Wyoming are more stoney than most. A very sandy soil develops about the stones that lie on the general soil surface; these small patches of "open" sandy soils are preferred sites for *Sedum lanceolatum* (cf. Table 1*a*).

Superficially at least, in some regions of *P. albicaulis* forests there appears to be taxonomic replacement within "life forms". *Arnica cordifolia* is generally prominent in those stands in which *A. latifolia* is not, and *Luzula hitchcockii* is relatively important in the Bitterroot Mts. where *Carex geyeri* is not.

Disjunctions. Daubenmire (1975) has applied the term "oceanic element" to taxa with distributions largely restricted to maritime-influenced climates of the Pacific Northwest (NW Montana, N Idaho, W Oregon, W and NE Washington and the adjacent parts of Alberta and British Columbia). I had considered both Xerophyllum tenax and Luzula hitchcockii to be strict oceanic elements, but their actual distributions are, in fact, more extensive. Widely disjunct populations of both species occur as far south as Teton Co., Wyoming (Shaw, 1976; Pfister et al., 1974; Maule, 1959). Menziesia ferruginea Smith and Pinus monticola Dougl. (not in whitebark pine forests) are other oceanic elements often found close to or associated with X. tenax and L. hitchcockii. They also have disjunct distributions nearly identical to the others (Hickman and Johnson, 1969; and personal observations). Perhaps in past times, the paleoclimate was sufficiently different to support an "oceanic" vegetation throughout the northern Rocky Mountains, as presently exists in NW Montana and N Idaho. Additional evidence for such a maritime paleoclimate is the discovery of *Taxus brevifolia* Nutt. (an unquestionably oceanic species) wood remnants during archaeological excavations in the Yellowstone Valley, SW Montana (Arthur, 1966; the same valley presently supports very localized populations of X. tenax and M. ferruginea). Radiocarbon dates for the Taxus materials were 5000 years BP (Such an age predates the well-known use of Taxus wood for archer's bows, thus long distance transport of the wood to this site is not likely.) The early Holocene epoch in the Rocky Mountains is thought to have been cool and wet (Hansen, 1947); the Xero- or Altithermal interval began about 7500 BP and lasted until the onset of Neoglaciation, ca. 4000 BP (Richmond, 1970), Wells (1970) has suggested that the "Xerothermal" interval in the Laramie Basin of Wyoming was wetter, not dryer, than present. Unless these plant disjunctions and excavations represent relict vegetation from pre-Pinedale Glacial times, with the recession of Cordilleran ice (12,000 BP; Richmond, 1970), a Pacific maritime climate and vegetation may have pervaded the entire northern Rocky Mountains. A subsequent cooling and drving trend in W Wyoming and SW Montana could not support a maritime vegetation, and extinctions and disjunctions resulted. High elevation bog pollen profiles in Yellowstone National Park (Waddington and Wright, 1974) are dominated by Pinus contorta from ca. 11,600 BP to present; an increase of Picea engelmannii pollen at 5000BP implies climatic cooling. That the W Wyoming-SW Montana area is still subjected to a relatively cold climate can be seen by the present gap in the distribution of Pinus ponderosa Laws. (Fig. 1), a typically "warm" pine (Mirov, 1967). Curiously, the absence of P. ponderosa from this area correlates generally with the occurrence of the P. albicaulis-V. scoparium association. If those whitebark pine stands with oceanic elements are omitted the correlation is nearly perfect.

Species Number. The number of species in the whitebark pine stands ranged from 6 in the oldest (640 years) to 33 in one of the youngest (33 years). There was a general trend in decreasing species number with stand age but stands that were proximal tended to have similar species numbers despite age differences.

Management Implications. Although whitebark pine forests receive relatively little resource management attention at present, this can be expected to increase rapidly. *P. albicaulis* produces exceptionally large mast crops (Forcella, 1977) and such production may significantly affect the habits of wildlife (Craighead, 1976; Forcella, 1977). Total net primary productivity in these forests may exceed 900 g/m²/yr. and standing crops may approach 60 kg/m² (Forcella and Weaver, 1977); economically these figures are substantial.

There are also some practical aspects involved with the floristic distributional anomalies of whitebark pine forests. The three dominant herbaceous species of the association are *Carex geyeri*, *Arnica latifolia* and *A. cordifolia*. These taxa all have known forage value for both domestic and wild ungulates. The biomass and energy (kcal) per unit area of each species can be readily predicted from their canopy coverages (measured separately; Forcella, 1977). Further, as can be seen in Table 1, the species have distributional limits within the association. If the 29 stands are split into three geographic/floristic regions (Fig. 1; separations based on plant distributions and agglomerative cluster analysis), the mean energy value per m² for each species differs significantly between at least two regions (t-test, p = 0.01). In vegetation mapping, the *P. albicaulis*-*V. scoparium* association as a whole would probably comprise a single cartographic unit. Knowledge of regional differences in forage availability within associations might prove valuable to resource managers.

Chorology. The stands shown in Fig. 1 essentially outline the distribution of the *P. albicaulis-V. scoparium* association. To the north and northwest, *Abies lasiocarpa, Larix lyallii* and *Vaccinium membranaceum* gain importance in whitebark pine forests. In Alberta, Canada (on acidic substrates), *P. albicaulis* occurs with equal amounts of *Picea engelmanii* and *A. lasiocarpa* in the overstory. Understory components always contain *V. scoparium*, but it may be accompanied or dominated by *Vaccinium caespitosum* Michx., *Empetrum nigrum* L., *Dryas octopetala* L., *Salix arctica* Pall., or *Spiraea* ssp. In Banff National Park, I found one stand on dolostone totally dominated by *P. albicaulis;* its understory, in order of importance, consisted of *Betula glandulosa* Michx., *Potentilla fruticosa* L., *Linnaea borealis* L., *Shepherdia canadensis* (L.) Nutt., *Juniperus communis* and *Dryas octopetala*. There were no vacciniums in this stand, probably due to its basic substrate.

The eastern limit of the *P. albicaulis–V. scoparium* association is correlated with the eastern extent of acid-rock mountain ranges in Alberta and Montana. Limestone ranges such as the Big Snowy Mountains (Montana) do not contain this association. The eastern limit in Wyoming is the Absaroka and Wind River Mountains; the granitic Big Horn Mountains, 170 km eastward, have only scattered populations of *P. albicaulis* (Hoffman and Alexander, 1976; D. Despain *pers. comm.*)

To the south, the Medicine Bow Mountains (Wyoming), the Colorado

MADROÑO

Rockies, and the Uinta Mountains of Utah all lack whitebark pine. That the southern limit of *P. albicaulis* coincides with the northern boundary of other edible large-seeded, grove-forming pines (*P. edulis* Engelm., S Wyoming; *P. monophylla* Torr. & Frem., S Idaho to California) may be more than coincidental. Forcella and Rumley (in prep.) hypothesize that prehistoric man carried seed of *P. sibirica* L. (= *P. albicaulis*) across Beringia. His dispersal of the energy-rich seed ceased when contact was made with native large-seeded pines.

In far western Wyoming (the Wyoming Range), *P. albicaulis* forests contain an understory of *Ribes montigenum* McClatchie (which forms conspicuous closed circles under the canopies of the rather widely spaced trees) and *Bromus carinatus*. To the northwest, in the White Cloud Peaks and Sawtooth Mountains of central Idaho, *P. albicaulis* stands often support an understory of *Artemisia tridentata* Nutt. and/or a carpet of forbs, *Lupinus argenteus* being the most prominent.

Within the distributional limits of the P. albicaulis -V. scoparium association, there may be other associations which contain P. albicaulis. On limestone outcrops, Weaver and Dale (1974) mention a stand in which P. flexilis James and various forbs associate with whitebark pine. I have seen such stands and others similar, but always including Arctostaphylos uva-ursi (L.) Spreng. This type of community, with a distinctly different habitat (limestone), appears to have been lumped with the P. albicaulis-V. scoparium association in the "habitat-type" classification of Pfister et al. (1974) and Reed (1976). Also, on what may be more mesic sites, Abies lasiocarpa shares the overstory with whitebark pine, and V. membranaceum is often present in the understory. It is possible that alternate plant associations (Abies vs. Pinus) may exist on the same site at different times, the occurrence of either possibly being a function of its seed crop size at the time of stand establishment. Seed production of P. albicaulis varies significantly from year to year (Forcella, 1977). A treeline form(s) of whitebark pine community occurs also; its distinguishing feature is, of course, the stunted growth and flagged structure of the trees (Daubenmire and Daubenmire, 1968). Clausen (1965) speculates a genetic basis for the stunted P. albicaulis of the Sierra Nevadan krummholz.

Conclusions

The *Pinus albicaulis–Vaccinium scoparium* association is limited to subalpine sites on non-calcareous substrates in western Wyoming, southwestern Montana and east-central Idaho. Its floristic composition changes clinally with latitude, but this does not necessarily imply a change in habitat. Nearly 25% of the taxa which comprise the association are distributionally restricted from occurring in all stands of the association. This suggests that to some degree the floristic composition of a stand is a function of the local flora available to it.

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LITERATURE CITED

- ARTHUR, G. W. 1966. An archaeological survey of the upper Yellowstone River Drainage, Montana. Mont. Agr. Exp. Stn. Econ. Res. Rept. 26, Bozeman. 199 pp.
- BOOTH, W. E. and J. C. WRIGHT. 1966. Flora of Montana, II. Montana State U., Bczeman. 305 pp.
- CLAUSEN, J. 1965. Population studies of alpine and subalpine races of conifers and willows in the California High Sierra Nevada. Evolution 19(1):56-68.
- CRAIGHEAD, J. 1976. Mapping grizzlies by satellite. Nat. Geographic 105(1):148-158.
- DAUBENMIRE, R. 1975. Floristic plant geography of eastern Washington and northern Idaho. J. Biogeography 2:1-18.

— and J. B. DAUBENMIRE. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agr. Exp. Stn. Bull. 60. 104 pp.

DAVIS, R. C. 1952. Flora of Idaho. Wm. C. Brown Co., Dubuque, Iowa. 828 pp.

- DESPAIN, D. G. 1975. Flora of Yellowstone National Park. Yellowstone Library and Museum Assoc. 155 pp.
- EGLER, F. E. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old field vegetation development. Vegetatio 14(6):412-471.
- FORCELLA, F. 1977. Flora, biomass and productivity of the *Pinus albicaulis-Vac*cinium scoparium association. Thesis, Montana State U., Bozeman.
 - and T. WEAVER. 1977. Biomass and productivity of the subalpine *Pinus* albicaulis-Vaccinium scoparium association in Montana, U.S.A. Vegetatio 35(2):95-106.
- HALE, M. 1969. The Lichens. Wm. C. Brown Co., Dubuque, Iowa. 226 pp.
- HANSEN, H. P. 1947. Postglacial forest succession, climate and chronology in the Pacific Northwest. Trans. Am. Phil. Soc. 37:1-130.
- HICKMAN, J. C. and M. P. JOHNSON. 1969. An analysis of geographic variation in Western North American Menziesia (Ericaceae). Madroño 20(1):1-11.
- HITCHCOCK, C. L. and A. CRONQUIST. 1973. Flora of the Pacific Northwest. U. of Washington Press, Seattle. 730 pp.
- HOFFMAN, G. R. and R. R. ALEXANDER. 1976. Forest vegetation of the Big Horn Mountains, Wyoming: A habitat type classification. USDA Forest Service Res. Paper RM-170, Rocky Mt. Forest & Range Exp. Stn., Fort Collins, Colorado.
- KING, T. T. 1977. The plant ecology of anthills in calcareous grassland II. Succession on the mounds. J. Ecol. 65:257–278.
- LITTLE, E. L. 1971. Atlas of United States Trees I, Conifers and Important Hardwoods. USDA Forest Service, Misc. Publ. 1146.
- MAJOR, J. 1951. A functional, factorial approach to plant ecology. Ecology 32: 392-412.

— and W. T. PYOTT. 1965. Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. Vegetatio 13:253–282.

MAULE, S. M. 1959. Xerophyllum tenax, squawgrass, its geographic distribution and its behavior on Mount Rainier, Washington. Madroño 15(2):39-48.

MIROV, N. T. 1967. The Genus Pinus. Ronald Press Co. New York. 602 pp.

- MUELLER-DOMBOIS, D. and H. ELLENBERG. 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons, New York. 547 pp.
- MUNZ, P. A. and D. D. KECK. 1968. A California Flora and Supplement. U. of California, Berkeley. 1905 pp.
- PFISTER, R. D., B. L. KOVALCHIK, S. F. ARNO and R. C. PRESBY. 1974. Forest Habitat Types of Montana. USDA Forest Service, Intermountain Forest and Range Exp. Stn. Missoula, Mont. 213 pp.

- RICHMOND, G. M. 1972. Appraisal of the future climate of the Holocene in the Rocky Mountains. Quat. Res. 2:315-322.
- SHAW, R. J. 1976. Field Guide to the Vascular Plants of Grand Teton National Park and Teton County, Wyoming. Utah State U. Press, Logan. 301 pp.
- SOIL SURVEY STAFF. 1975. Soil Taxonomy. USDA Soil Conservation Service, Agr. Handbook 436. 754 pp.
- WADDINGTON, J. B. and H. E. WRIGHT. 1974. Late Quaternary vegetation on the east side of Yellowstone National Park, Wyoming. Quat. Res. 4:175-184.
- WELLS, P. V. 1970. Postglacial vegetational history of the Great Plains. Science 167:1574–1582.
- WESTHOFF, V. and E. VAN DER MAAREL. 1973. The Braun-Blaunquet approach. In Handbook of Vegetation Science V: Ordination and Classification of Communities. R. H. Whittaker (ed.), pp. 617-726. W. Junk Publ., The Hague.

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Errata, Madroño, volume 24

- p. 140. Seventh line from bottom should read "Cactáceas" for "Cactácea".
- p. 141. Second line should read "segmentisque" for "sementisque", "enationibus" for "enatioaibus", and "filamentis" for "filamentis".
- p. 145. Last line should read "synonymy" for "snyonymy".
- p. 150. Sixth line from bottom should read "Mason" for "Masin".
- p. 155. Thirteenth line should read "filamentisque" for "filimentisque".
- p. 156. Third paragraph, third line, should read "collections" for "collection".